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QUANTITATIVELY SAMPLING LAND-SNAIL SPECIES RICHNESS IN MADAGASCAN RAINFORESTS

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ABSTRACT

Land-snail species richness in tropical rainforests tends to be high but difficult to assess because of low densities and often small shell sizes. We tested three quantitative sampling methods in primary rainforests of southeastern Madagascar. Timed searching yielded seven times as many micro-snail species (species that during at least part of their life have shells < 5 mm maximum dimension) per person-hour as either litter sampling or soil-plus-litter sampling. The number of species found in 20 m × 20 m during three person-hours of searching, however, was boosted a maximum of 38% by one eight-liter sample each of litter and soil-plus-litter. Litter sampling and timed searching both yielded more than 1.5 times the proportion of live-collected species as soil-plus-litter sampling. Sampling method was unbiased toward 12 of the 20 commonest species, but three large, presumed arboreal species were favored by timed searches; two minute, presumed burrowers by soil-plus-litter sampling; and three minute, cryptically colored species by both litter and soil-plus-litter sampling. A 1.2-mm sieve caught at least 78% of the total specimens and passed adults of 7% of species, of which the smallest adult dimension was 1.0 mm. These results suggest that the best sampling strategy is timed searching for micro-snails, while incidentally collecting macro-snails and litter-plus-soil for later picking of the 5.5–1.2 mm and the 1.2–0.85 mm, dry-sieved fractions. This strategy should be transferable to other tropical-rainforest land-snail faunas.

Key words: Gastropoda, tropical biodiversity, leaf-litter biota, soil biota.

INTRODUCTION

Land snail faunas of tropical rainforests tend to be quite diverse (maximum reported: 52 species per 4 ha) despite often low densities (Emberton, 1995a [and citations therein]; Tattersfield, 1994, in prep.; F. Thompson, pers. commun.; despite Solem's [1984] undocumented statement to the contrary). Much of this diversity consists of micro-gastropods (< 5 mm greatest dimension), the collection of which can be extremely labor-intensive (Emberton, 1994, 1995a, 1996; DeWinter, 1995; F. Thompson, pers. commun.; P. Tattersfield, pers. commun.; R. Ramirez, pers. commun.). Because most tropical rainforests are vastly undercollected for micro-gastropods and are undergoing irreversible deforestation, great urgency attaches to collecting these mostly undiscovered, undescribed molluscs as efficiently and thoroughly as possible. Because of the prime importance in land-snail systematics of preserving anatomies and DNA in ethanol, sampling methods should maximize live collections. Because land snails are generally so patchily distributed, even within seemingly uniform forest, sampling should probably avoid random-quadrat methods (Emberton, 1995a).

Timed searches by experienced collectors are a well-proven method of quantitatively sampling patchily distributed organisms (Coddington et al., 1991). One of us has recently advocated timed searches as the most efficient collecting method for tropical rainforest micro-snails (Emberton, 1995a), and has applied such data toward assessing conservation priorities (Emberton, 1996). The efficacy of timed searches for collecting all or a substantial portion of the micro-gastropod fauna, however, has never been tested, to our knowledge.

Collection of measured quantities of selected leaf litter is another quantitative sampling method that has proven effective for tropical-rainforest land-snail communities (Tattersfield, 1994). Soil-plus-litter samples also often yield species that are collected in no other way (F. Thompson, 1995). Some species may be soil specialists, other species may take refuge in soil from drying litter, and soil can accumulate dead shells of litter spe-

cialists (pers. observ.; Burch & Pearce, 1990). Processing of soil-plus-litter samples, however, is more labor-intensive than processing of litter samples.

The purpose of this paper is to compare the performances of (a) timed searching, (b) litter sampling, and (c) soil-plus-litter sampling for determining the species richness of and obtaining live material of the micro-land-snail fauna of Madagascan rainforests, and to arrive thereby at the most efficient overall sampling strategy.

METHODS AND MATERIALS

We sampled 48 plots, each 20 m × 20 m, at 16 stations on three widely separated mountains in southeastern Madagascar (Fig. 1, Table 1). Localities and stations were chosen to serve both for this study and for testing diversity patterns between the Vohimena and Anosy mountain chains (Emberton, 1996, Emberton et al., in review). Stations were at 100 m elevation intervals from 100 m to 500 m and at 200 m elevation intervals above 500 m, with a station at the highest or a local summit.

Stations were restricted to primary forest that had no more than limited selective cutting. For each station, we recorded the elevation (average of two Thommen Altitrek altimeters, calibrated from topographic maps), latitude and longitude (from topographic maps), and the topography (summit, ridge, slope, or valley). For more extensive data on these stations, see Emberton (in review).

At each station, we sampled three adjacent 20 m × 20 m replicate plots, each marked off with flagging tape. We sampled 25 January to 7 February 1995, during the rainy season, within one week of heavy rains, when snails and slugs seemed likely to be most active and therefore perhaps easier to find. We included only micro-snails, which for the purposes of this study we defined as those species that during at least part of their life have shells that are smaller than 5 mm maximum dimension (the vast majority remain below this size as adults).

Timed searching was for three person-hours per plot: one-half hour by six collectors. Three of these collectors (RR and two assistants who had been trained by all three authors) were constant over all stations and plots, and the other three were hired locally and trained by RR. As incentives, small cash prizes were offered for the most snails and the smallest snail collected in each plot. Micro-molluscs were hand-collected into 30-ml, snap-cap vials, drowned overnight, then fixed and preserved in 70–90% ethanol.

Litter samples and soil-plus-litter samples were each eight l in volume per plot, collected over a 30-minute period by KCE and TAP, respectively. Both types of sampling were from moist, sheltered microhabitats such as beside logs, between buttress roots of trees, within *Asplenium* and *Pandanus* rosettes, under and near piles of *Ravenala* and palm fronds, and in moist depressions (Emberton & Arijaona, in press: fig. 2). Litter and litter-plus-soil samples were collected into four-mill plastic bags and kept as cool as possible until processing, a maximum of three days later, with daily opening of each bag for aeration.

All litter and soil-plus-litter samples were wet-sieved through three mesh sizes: 11.5 mm, 5.5 mm, and 1.2 mm. We used wet sieving (i.e. washing the samples with water) in order to process quickly samples wet from recent or current rains, and to assure live recovery of slugs, semislugs, and thin-shelled species. Sieve boxes for the first three size fractions consisted of large plastic storage boxes (55 × 48 × 35 cm) from which the bottoms had been cut (leaving a 3.8-cm margin), then covered with hardware cloth (11.5 mm), hardware mesh (5.5 mm), or hardware screen (1.2 mm) (the latter two supported by hardware cloth) held in place with duct tape. The three sieve boxes were nested over an intact box to catch effluent during washing of a litter sample and were transferred to a second box if the first filled. Whenever the litter or soil-plus-litter samples were not too wet, as much dry-sieving as possible was performed prior to wet-sieving. The first two sieve fractions were picked immediately for all invertebrates by the authors, aided by teams of local workers, each of whom was carefully trained and monitored by at least one of the authors. The third fractions (retained by the 1.2-mm sieve) were fixed and stored for no longer than three weeks in an equal or greater volume of 90% ethanol (the resulting ethanol concentration averaged about 60%). The effluent was caught by pouring all sieved wash water from the bottom box or boxes through two nested nylon stockings, from which excess water was squeezed gently, then which were fixed and stored in an equal or greater volume of 90% ethanol.

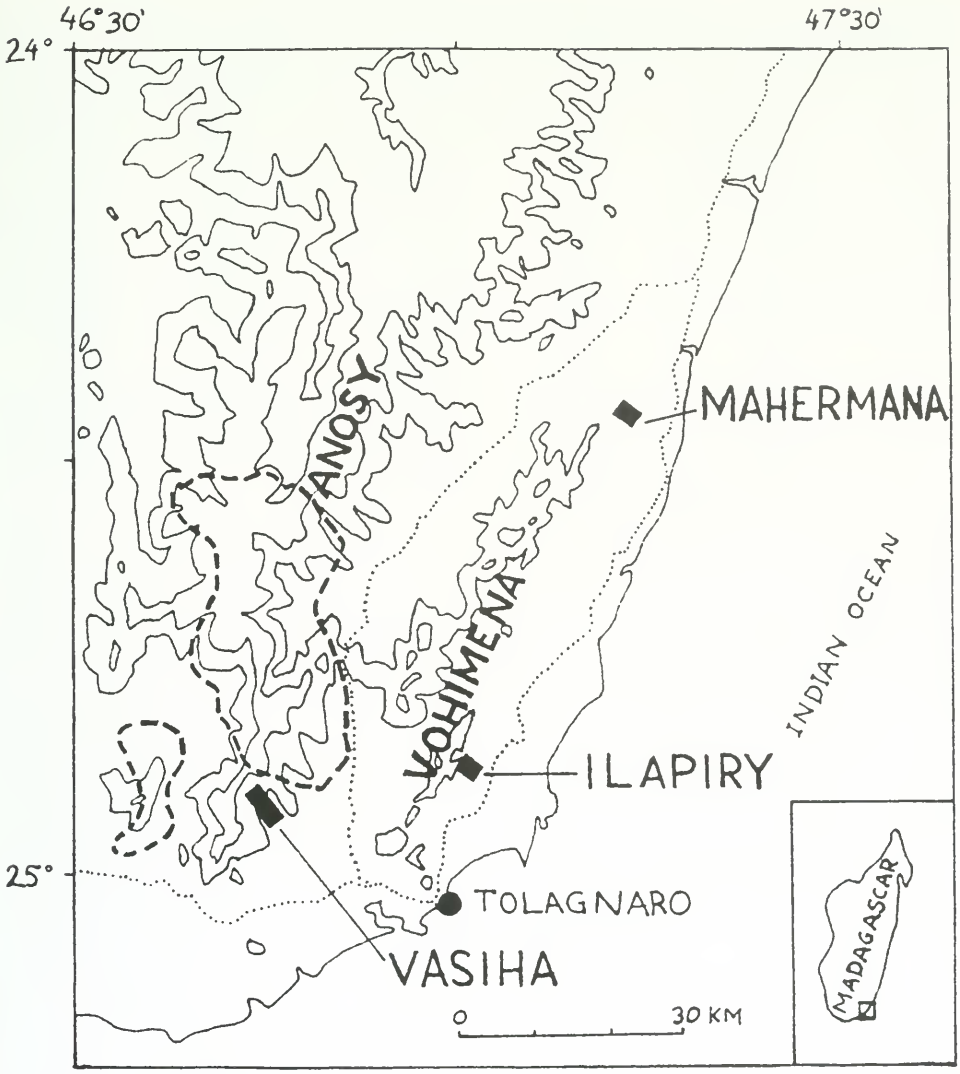

FIG. 1. The three mountains sampled in the Anosy and Vohimena chains, southeastern-most Madagascar (see inset). Contours are shown at 500 m and 1,000 m. The dashed line indicates Andohahela Reserve. The dot indicates the city of Fort Dauphin (= Tolagnaro).

All > 1.2-mm sieve fractions were picked for all invertebrates by RR and six assistants, each of whom was trained by all three authors and monitored by RR. Non-molluscan invertebrates are being distributed among interested specialists. Only molluscs are analysed in this paper.

To test the efficiency of the 1.2-mm sieve at catching snails, the sieving effluent (i.e., all that passed through the 1.2-mm sieve) from one plot per station (the plot whose upper sieve fractions yielded the greatest number of species) was further sieved through U.S.A. Standard Testing Sieves Nos. 20 and 30 (0.85 mm and 0.60 mm). Both these fine fractions were picked for snails and shells by RR and four trained, monitored assistants, wearing Optivisor magnifying lenses of 2× magnification. Picking of all sieve fractions was performed on a white or light-gray, hard surface. Those snails from the < 1.2 mm fraction were used only for testing the sieve effi-

TABLE 1. Stations sampled for land snails in southeastern Madagascar. Elv = elevation in meters, r/s/v = ridge, slope, and valley.

#	Mountain	Elv	Latit. S	Long. E	Topogr
1	Mahermano	340	24.26.12	47.13.13	summit
2	Mahermano	300	24.26.17	47.13.10	slope
3	Mahermano	200	24.26.15	47.13.04	slope
4	Mahermano	100	24.26.22	47.12.41	valley
5	Ilapiry	540	24.51.40	47.00.20	summit
6	Ilapiry	500	24.51.33	47.00.27	ridge
7	Ilapiry	400	24.51.27	47.00.38	r/s/v
8	Ilapiry	300	24.51.36	47.00.40	slope
9	Ilapiry	200	24.51.39	47.00.46	slope
10	Vasiha	860	24.55.18	46.44.19	summit
11	Vasiha	700	24.55.23	46.44.27	slope
12	Vasiha	500	24.55.19	46.44.45	slope
13	Vasiha	400	24.55.25	46.44.45	valley
14	Vasiha	300	24.55.37	46.44.49	slope
15	Vasiha	200	24.56.13	46.45.13	slope
16	Vasiha	100	24.56.20	46.46.07	slope

ciency, and were not included in the main data matrix or data analysis.

All snails and shells were sorted and identified to morphospecies by KCE. For each morphospecies, a relatively intact adult representative was chosen and was photographed in two to five diagnostic views at standard magnifications, using a Polaroid camera mounted on a Wild dissecting microscope. The resulting reference collection and file of photographs were used to identify all specimens, both adults and juveniles, except for some juveniles of the most minute sieve fractions, which were identified only to genus or family. Systematic treatments of the morphospecies, 85% of which are new, are in progress; vouchers are in the collection of the Molluscan Biodiversity Institute, with types and references to be placed in the Madagascar national museum (Parc Botanique et Zoologique de Tsimbazaza, Antananarivo) and in the Academy of Natural Sciences of Philadelphia. (Patterns of diversity, distribution, and abundance of the morphospecies are treated in a separate paper [Emberton, in review].)

To compare efficiencies of the three methods, we calculated the number of person-hours required to collect and—in the case of litter and litter-plus-soil—to wet-sieve and to pick an average sample (for all invertebrates). We then computed the mean numbers of molluscan specimens and of species obtained per person hour by each method. We were not able to calculate the percent of picking time devoted to molluscs alone, so our person-hour calculations were overestimates.

We used analysis of variance (ANOVA) by least-squares estimation (Wilkinson, 1990) to evaluate differences among the three sampling methods in (a) number of species collected per plot, (b) percent of the total species that were found in each plot, and (c) percent of species collected live. For the percent of the total species collected within each plot, we used the entire data set in a one-way ANOVA. For species number and percent live, however, we factored out the effects of locality (mountain) and elevation by including them in a three-way ANOVA on the largest possible subset of the data including all three mountains (see Emberton et al., in review: fig. 2), which had to be limited to 200 m and 300 m elevations (Table 1).

For each species representing at least one percent of the total specimens, we used chi-square analysis to test among the three sampling methods for equal numbers of specimens. Predicted frequencies were based on the total number of specimens resulting from each method. Probability estimates were Bonferroni-adjusted to allow for multiple tests.

RESULTS

Including the macro-snail species that showed up in the upper sieve fractions, we collected a total of 87 species (also see below). Taxonomically, these species were dis-

TABLE 2. Average time investments and productivities of three sampling methods. Collect = collecting within a 20 m × m plot, Sieve = wet sieving of an eight-liter sample from a 20 m × 20 m plot, Pick = picking all invertebrates (not just gastropods) from the > 1.2-mm sieved sample, Total hours = total person-hours per plot sample, Specm./p-hr = mean number of specimens obtained per person hour, Spp./p-hour = mean number of species obtained per person hour, Spp./specm. = proportion of mean species to mean specimens.

Method	Person-Hours per Task			Total hours	Specm. p-hr	Spp./ p-hr	Spp./ specm.
	Collect	Sieve	Pick				
Timed search	3.0	0.0	0.0	3.0	9.36	3.03	0.32
Litter sample	0.5	4.8	4.7	10.0	0.88	0.46	0.52
Soil-plus-litter	0.5	4.8	9.8	15.1	0.91	0.41	0.45

tributed as follows, with higher classification following Abbott & Boss (1989) for "Prosobranchia" and Gymnomorpha and Nordsieck (1986) for Pulmonata:

"Subclass PROSOBRANCHIA"
  Order MESOGASTROPODA
    Superfamily CYCLOPHOROIDEA
      Cyclophoridae
        Boucardicus 17
        Cyathopoma 1
        Hainesia 1
    Diplommatinidae
        Malarinia 1
  Superfamily LITTORINOIDEA
      Pomatiasidae
        Tropidophora 3
  Superfamily RISSOOIDEA
      Assimineidae
        Omphalotropis 2
Subclass GYMNOMORPHA
  Order SOLEOLIFERA
      Veronicellidae 1
Subclass PULMONATA: Order STYLOMMATOPHORA
  Suborder ORTHURETHRA
    Superfamily CHONDRINOIDEA
      Orculidae
        Fauxulus 2
  Suborder SIGMURETHRA
  Infraorder ACHATINIDA
    Superfamily ACHATINOIDEA
        Subulinidae 3
    Superfamily STREPTAXOIDEA
        Streptaxidae 14
    Superfamily ACAVOIDEA
      Acavidae
        Ampelita 1
        Clavator 1
        Helicophanta 1
    Superfamily PUNCTOIDEA
        Charopidae 9
Infraorder HELICIDA
  Superfamily HELICARIONOIDEA
    Helicarionidae: Sesarinae
      Kaliella 1
    Helicarionidae: Microcystinae
      Microcystis 10
    Helicarionidae: Ariophantinae
      Kalidos 7
      Malagarion 1
    Helicarionidae: Macrochlamydinae
      Sitala 9

We excluded from analysis all specimens of the one slug species (Veronicellidae) and of the six snail species that were considered always too large, even as juveniles, to qualify as micro-molluscs (< 5 mm): the one *Hainesia,* two of the three *Tropidophora,* and all three acavids.

Distributions of the 80 analyzed species among samples, totalling 2,430 specimens, are archived at the Molluscan Biodiversity Institute (MBI) and the Academy of Natural Sciences of Philadelphia (ANSP).

The three sampling methods required drastically different investments of time to acquire gastropods (Table 2). Timed search was by far the most efficient, yielding about ten times the number of specimens and seven times the number of species per person-hour as either litter sampling or soil-plus-litter sampling. These advantages are inflated somewhat, however, because we took time to pick all invertebrates.

The litter and soil-plus-litter methods were more diverse than timed search, yielding about half again as many species per specimen (also see below).

Table 3 gives ANOVA results for number of species collected per 20 m × 20 m plot. Sampling method had a highly significant effect when the less significant effect of elevation

TABLE 3. Analysis of variance in the number of species collected per 20 m × 20 m plot, with least-squares estimates of means. Independent variables are sampling method (timed search vs. litter sample vs. soil-plus-litter sample), elevation (200 m vs. 300 m), and location (one of three mountains).

Source	Sum of Squares	Degrees of Freedom	Mean Square	F-Ratio	Probability of Equality
Sampling	172.0	2	86.0	16.83	0.000***
Elevation	29.6	1	29.6	5.80	0.021*
Locality	28.3	2	10.2	1.99	0.152
Sam × Elv	16.1	2	8.1	1.58	0.220
Sam × Loc	38.3	4	9.6	1.88	0.136
Elv × Loc	0.9	2	0.5	0.09	0.914
S × E × L	10.6	4	2.7	0.52	0.722
Error	184.0	36	5.1		

	Number of Species		
	Mean	Std. Error	N
Sampling:			
Timed	9.0	0.5	18
Litter	4.7	0.5	18
Soil-Lit	6.3	0.5	18
Elevation:			
200m	7.4	0.4	27
300m	5.9	0.4	27
Locality:			
Mahermano	5.9	0.5	18
Ilapiry	7.4	0.5	18
Vasiha	6.6	0.5	18

*$p < 0.05$, *** $p < 0.001$.

was partitioned out (see Emberton et al., in review, concerning elevational variation). Timed searching within 20 m × 20 m for three person-hours averaged 9.0 species. This was about twice as many species as occurred in an eight-liter sample of litter selected from the same area (4.7 species), and was about half again as many species as occurred in an equivalent soil-plus-litter sample (6.3 species). Thus, this timed searching method produced more species than the other two sampling methods. When considered in the context of time invested, the productivity of timed searching by this method was even more pronounced (see above).

Timed searching alone, however, fell far short of assessing total number of species collected. ANOVA results in Table 4 indicate that timed searching produced on average only 72% of the species sampled within a 20 m × 20 m plot. Thus, the number of species found in a plot during three person-hours of searching was boosted 39% (28%/72%) by one eight-l sample each of litter and soil-plus-litter. Most of these additional species occurred in soil-plus-litter samples, which yielded half of the total, as opposed to the litter samples, which yielded only somewhat over a third of the total sampled species.

On the other hand, Table 5 shows that for sampling live-collected individuals, litter sampling was equivalent to timed searching ($51.6 \pm 5.6 = 46.4 \pm 5.2$) and significantly more efficient than soil-plus-litter sampling. Thus, nearly half of the litter-sample and timed-search species were represented by at least one live-collected individual, whereas only somewhat over a fourth of the soil-plus-litter-sample species were. This result was not surprising because soil can accumulate dead shells of snails living in litter or trees (pers. observ.; Burch & Pearce, 1990). In other words, litter sampling and timed searching both yielded more than 1.5 times the proportion of live-collected species as soil-plus-litter sampling.

Table 6 shows the total live-plus-dead number of each species collected by each of the three sampling methods. Twenty species (25%) were represented by at least 1% (> 24) of the total specimens. Chi-square tests on these species indicated that 12 (60%) of them had equal (not significantly different) representation among sampling methods. Of

TABLE 4. Analysis of variance in the percent of species that were collected within each replicate plot, with least-squares estimates of means. the independent variable is sampling method (timed search vs. litter sample vs. soil-plus-litter sample).

Source	Sum of Squares	Degrees of Freedom	Mean Square	F-Ratio	Probability of Equality
Sampling	30,530.9	2	15,265.4	49.1	0.000***
Error	43,868.3	141	311.1		

	Percent of Species		
	Mean	Std. Error	N
Sampling:			
Timed	72.4%	2.5%	48
Litter	37.1%	2.5%	48
Soil-Lit	50.1%	2.5%	48

*** $p << 0.001$.

TABLE 5. Analysis of variance in the percent of species represented by at least one live-collected individual, with least-squares estimates of means. Independent variables are sampling method (timed search vs. litter sample vs. soil-plus-litter sample), elevation (200 m vs. 300 m), and location (one of three mountains).

Source	Sum of Squares	Degrees of Freedom	Mean Square	F-Ratio	Probability of Equality
Sampling	5057.0	2	2528.5	5.24	0.010**
Elevation	165.1	1	165.1	0.34	0.562
Locality	922.9	2	461.5	0.96	0.394
Sam × Elv	381.0	2	190.5	0.40	0.677
Sam × Loc	1446.5	4	361.6	0.75	0.565
Elv × Loc	712.9	2	356.4	0.74	0.485
S × E × L	2627.2	4	656.8	1.36	0.268
Error	16405.0	34	482.5		

	Percent Live Species		
	Mean	Std. Error	N
Sampling:			
Timed	46.4%	5.2%	18
Litter	51.6%	5.6%	16
Soil-Lit	28.4%	5.2%	18
Elevation:			
200m	43.9%	4.5%	25
300m	40.3%	4.2%	27
Locality:			
Mahermano	47.8%	5.4%	17
Ilapiry	41.3%	5.2%	17
Vasiha	37.3%	5.4%	17

** $p = 0.01$.

the remaining eight species, *Boucardicus* sp. 9 and *Microcystis* sp. 4 were significantly more prevalent in both litter and soil-plus-litter samples than in timed-search samples, and *Sitala* sp. 7 was present in the litter samples in greater proportions than expected in the chi-square test. All three of these are both dark brown in color (matching the color of litter and soil) and minute in size (adult greatest dimensions 2.2 mm, 2.2 mm, and 1.8 mm, respectively).

Two species—Streptaxidae spp. 9 and 13—were predominant in soil-plus-litter samples and notably scarce in litter only samples. Both these species are high-spired (height/diameters 2.5 and 2.2), very small (adult

TABLE 6. Numbers of snails of each of 80 species collected using three different sampling methods: t = timed search, l = litter sample, s = soil-plus-litter sample. Chi-square tests for equal frequencies among sampling methods were calculated for each species with > 24 specimens: * $p < 0.05$, Bonferroni adjusted. GnSp = genus or family and numbered morphospecies. Genera and families in taxonomic order are: BO, *Boucardicus;* CY, *Cyathopoma;* MN, *Malarinia;* TR, *Tropidophora;* OM, *Omphalotropis;* FA, *Fauxulus;* SU, Subulinidae; ST, Streptaxidae; CH, Charopidae; KL, *Kaliella;* MI, *Microcystis;* KD, *Kalidos;* MG, *Malagarion;* and SI, *Sitala.*

	Number						Number				
GnSp	t	l	s	Total	Chi-Sq	GnSp	t	l	s	Total	Chi-Sq
BO01	131	35	43	209	5.4	CH01	28	4	3	35	9.0
BO02	47	11	15	73	2.5	CH02	75	34	59	168	8.2
BO03	3	0	2	5	—	CH03	6	0	3	9	—
BO04	11	5	8	24	—	CH04	14	1	12	27	5.9
BO05	2	0	1	3	—	CH05	14	2	5	21	—
BO06	6	3	0	9	—	CH06	18	2	8	28	2.1
BO07	32	10	9	51	2.4	CH07	3	0	0	3	—
BO08	2	0	3	5	—	CH08	1	0	0	1	—
BO09	1	*39*	*33*	73	102.3*	CH09	4	0	0	4	—
BO10	1	1	1	3	—	KL01	8	6	1	15	—
BO11	7	0	5	12	—	MI01	15	3	4	22	—
BO12	1	0	1	2	—	MI02	7	0	1	8	—
BO13	5	5	6	16	—	MI03	31	9	14	54	0.1
BO14	2	2	2	6	—	MI04	1	*9*	*20*	30	34.6*
BO15	0	1	0	1	—	MI05	1	0	2	3	—
BO16	1	1	0	2	—	MI06	2	1	0	3	—
BO17	0	1	0	1	—	MI07	0	1	0	1	—
CY01	13	9	12	34	4.3	MI08	2	4	2	8	—
MN01	0	0	1	1	—	MI09	3	2	0	5	—
TR01	*195*	20	56	271	33.0*	MI10	2	0	1	3	—
OM01	0	1	2	3	—	MI11	1	0	0	1	—
OM02	1	7	1	9	—	MI12	1	0	0	1	—
FA01	1	2	1	4	—	KD01	*105*	9	21	135	27.7*
FA02	0	0	1	1	—	KD02	22	2	0	24	—
SU01	104	18	54	176	6.3	KD03	7	1	0	8	—
SU02	3	2	2	7	—	KD04	6	4	0	10	—
SU03	2	5	6	13	—	KD05	1	0	0	1	—
ST01	9	0	1	10	—	KD06	7	1	1	9	—
ST02	6	1	3	10	—	KD07	9	11	1	21	—
ST03	11	2	0	13	—	MG01	9	3	1	13	—
ST04	9	3	8	20	—	SI01	11	5	3	19	—
ST05	2	0	0	2	—	SI02	7	0	3	10	—
ST06	88	25	53	166	2.0	SI03	1	1	4	6	—
ST07	20	2	7	29	2.9	SI04	5	1	3	9	—
ST08	13	1	4	18	—	SI05	*49*	0	2	51	34.2*
ST09	13	1	*25*	39	27.8*	SI06	4	0	0	4	—
ST10	2	11	7	20	—	SI07	102	*70*	*78*	250	27.8*
ST11	2	2	5	9	—	SI08	1	0	0	1	—
ST12	6	1	3	10	—	SI09	0	0	1	1	—
ST13	10	8	*27*	45	26.7*						
ST14	3	0	1	4	—	Tot	1348	420	662	2430	

heights 3.9 mm and 3.6 mm), and with glossy, fusiform, small-apertured shells suggestive of a soil-burrowing niche. In contrast, *Tropidophora* sp. 1, *Kalidos* sp. 1, and *Sitala* sp. 5 all occurred predominantly in timed searches and were significantly under-represented in litter and soil-plus-litter samples. All three of these species are relatively large (adult greatest dimensions 13.1 mm, 33.5 mm, and 7.3 mm). *Tropidophora* sp. 1 is often if not exclusively arboreal, and *K.* sp. 1 juveniles are at least partially arboreal, as they frequently show up in vegetation-beating samples (Emberton, unpublished); *S.* sp.

5 has a fragile, light-colored shell that is high-spired for the genus (height/diameter 1.0), all suggestive of arboreality.

A total of 101 specimens passed through the 1.2-mm sieve. (Distributions of these specimens among species and samples are archived at MBI and ANSP.) Thus, the 1.2-mm sieve caught a minimum of 78% of the specimens in the litter and litter-plus-soil samples of each plot.

The 1.2-mm sieve caught representatives of all species in the samples, however, except for one: Streptaxidae sp. 15. This is a minute, high-spired species (adult height 2.4 mm, diameter 1.0 mm), of which only two specimens were obtained. In addition, the sieve passed at least one adult of the five smallest species of *Boucardicus*, some in substantial numbers. Thus, adults of six species (8% of total) passed through the sieve at least in part. The smallest adult dimension of any of these species was 1.0 mm.

DISCUSSION

Sieving of litter and litter-plus-soil may at first seem superior to timed searches for sampling land-snail diversities because it yields higher ratios of species to individuals. Practically, however, timed searches are the most expedient by far, yielding species at 6.6 times the rate per person hour of either sieved sampling method. The degree of this advantage is surely an overestimate, because of our labor-intensive method of wet-sieving then picking for all invertebrates; nevertheless, even if we could halve or quarter our litter-processing time, time searching would be 3.3 or 1.7 times as efficient. Timed searching also requires minimal equipment and minimal weight and volume of samples to transport (critical factors in expeditions that require extensive backpacking).

Nevertheless, our method of timed searching yielded fewer than three-fourths of the total species collected per plot. A more thorough sampling strategy must, therefore, include some litter or soil-plus-litter sampling. Both these methods were roughly equivalent in their species richness and number of specimens per person-hour of effort. There were different advantages to each. Litter samples were 50% faster to process and yielded more live-represented species, whereas soil-plus-litter samples collected burrowing species that were otherwise missed. Thus a sample of litter-plus-soil seems preferable.

Thus, for greatest efficiency in assessing species number and obtaining live specimens, a good strategy seems to be collecting litter-plus-soil samples during timed searches, taking them from places that are yielding good numbers of micro-molluscs. To be quantifiable, samples should be taken to a constant or measurable volume.

Because only minute, cryptic or burrowing species were missed by timed searching, because the 1.2-mm sieve passed both adults and identifiable juveniles, and because 1.0 was the smallest adult dimension we encountered, we recommend in processing the supplemental litter-plus-soil samples that the 5.5-mm sieve fractions be discarded, and that both the > 1.2-mm and the > 0.85-mm fractions be retained and picked for micro-molluscs. Only a few of the minutest juveniles will be missed, at least for these Madagascar samples. Because wet-sieving is very labor-intensive (Table 2) and logistically difficult, we recommend dry-sieving, either on-site when litter and soil are dry enough, or later when the samples have been stored in, for example, muslin bags long enough to dry sufficiently without dehydrating slugs and semi-slugs.

Macro-molluscs (young juveniles > 5 mm) tend to comprise only a small part of the Madagascan rain-forest land-snail fauna, in this case 7% (6/88) of the species. Also, macro-snails have been the most extensively collected in the past (Emberton, 1995b), so are least likely to yield new biogeographic or systematic information. Therefore, for greatest efficiency in sampling total species richness, we recommend emphasizing the collection of micro-snails, and collecting macro-snails only as they are encountered during micro-snail searches.

Thus, in sum, timed searches for micro-snails, incidentally collecting macro-snails and litter-plus-soil for dry-sieving and picking the > 1.2-mm and > 0.85-mm fractions, seem best for quantitatively sampling Madagascan rainforest land-snails. This strategy should be transferable, with local modifications, to other tropical rainforests.

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